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Fauna of the Canal Zone indicates separation of Central and South America during most of the Tertiary.

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The fossil mammal faunas of North and South America indicate that the two continents were separated from Paleocene or earlier time until the late Pliocene (*1*, *2*). Unfortunately our almost complete ignorance of the Tertiary land mammals of Central America, together with incomplete knowledge of the geology of this large area, makes reconstruction of the Tertiary zoogeography of the region between the continents an exercise involving considerable speculation. While the differences between the faunas of the two continents, resulting from complete and long separation, prove the existence of one or more straits of some size between North and South America, we are uncertain as to the number of straits, their location, and the time of their existence. It is almost certain that there were straits across the Isthmus of Panama (*3*), and the distribution of Tertiary marine deposits indicates a major seaway in northwestern Colombia, the Bolivar Trough (Fig. 1). Thus, the separation of North from South America did not depend on the opening of a single strait. In Central America as a whole, however, the distribution of land and water during Tertiary time can be only approximately delineated, because geologic observations, as well as fossil finds, are relatively few and scattered over a large tropical region where there are few rock outcrops. A difficulty that faces the paleogeographer studying the isthmian portion of Central America is

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the large amount of tectonic activity that characterizes it to this day. In this the student of the Isthmus of Panama has problems in common with the paleogeographer who tries to unravel the history of an island arc. We know that faulting and folding were practically continuous in the isthmian area for a long time, thus it is risky to postulate the stability required for the existence of a land bridge (we use the term in its literal sense). It is more likely that the area of the Isthmus of Panama was characterized through most of the Tertiary by a shifting pattern of island groups and of peninsulas attached to one continent or the other.

An attempt to reconstruct the paleogeography of the Isthmus of Panama almost inevitably starts with consideration of the Canal Zone. As a result of the construction and maintenance of the Canal, the geology of the Zone is better known than that of the rest of Central America (*4*, p. 2). Marine and brackish-water beds of Eocene to Pliocene age have been described. From their distribution across the narrow isthmus it is reasonable to assume that these beds were deposited in a Tertiary seaway that can appropriately be called the Strait of Panama. The invertebrate fauna found in these beds permits an age definition of the strait that embraces the period during which the North and South American mammal faunas were separated from each other and thus pursued divergent evolutionary paths. However, when one attempts to define very closely the time of opening or closing of this strait, or to determine whether it opened and closed more than once, or even to determine precisely where it was, lack of data prevents the formulation of a precise answer. Thus, isolated fossil finds, even of poorly preserved material, and correlations over long distances assume greater importance in studying the Panama area than would be accorded such information in most geologic studies.

Because of this paucity of fossils, students of the terrestrial zoogeography of Central America have been forced to reconstruct the history of the area largely on the basis of the distribution of the modern fauna. Darlington (*5*, p. 285) believes that Central America was probably completely cut off by water from North as well as South America through much of the Tertiary. "My reason for thinking this," he says, "is that many of the older West Indian vertebrates seem (judging from their patterns of distribution on the islands) to have come from Central America, and they include animals, especially hystricomorph rodents, of sorts which would probably not have been in Central America if it had been connected to North America." Darlington thus regards Central America as having been an island in Tertiary time, from which animals migrated eastward into the West Indies. Simpson, on the other hand, is of the opinion (*1*, p. 388) that "with local and geologically brief interruptions for part of it, Central America has been continuous with the North American land mass throughout the Cenozoic." This conclusion is also based largely upon analysis of the living fauna of the region. Both these authors regard Central (or, more broadly, Middle) America as an evolutionary center.

Fossil Mammals of the Cucaracha Formation

In contrast to the abundance of Tertiary invertebrates in the Isthmus of Panama, only a few scraps of terrestrial mammal bones had been found there until recently, despite many years of intermittent prospecting (*4*, p. 37). In 1962 Stewart discovered fragmentary but identifiable mammal bones in an area of Miocene terrestrial deposits that had been exposed in the course of engineering operations along the right-of-way of the Panama Canal. Assisted by Joanne Allen, he collected the first of about 100 fragments of mammal bone from the Cucaracha Formation, a unit consisting mainly of bentonitic clay and siltstone. The fossil bones are found over an area about 2/5 kilometer long, parallel to the Canal in Gaillard Cut; the belt of outcrop is about 90 meters wide. In this area the Cucaracha Formation dips about 30° to the southwest. The fossil bones are weathered out on the surface or in the slightly weathered clay near the surface of the outcrop. They appear to occur in several bands 1.2 to 1.5 meters thick distributed through a stratigraphic thickness of some 45 meters.

The Cucaracha bones are the first identifiable Tertiary mammal remains found between Honduras and Colombia and the first Miocene mammal fossils found between southern Mexico and Colombia, a distance by land of some 2000 kilometers. They are the second discovery of Miocene land mammals in Middle America. The collection also includes bones of turtles, part of the skeleton of a large crocodile, and innumerable coprolites. The mammals in the fauna are of undoubted North American affinity. Four mammalian families are represented: the Equidae, the Rhinocerotidae, the Merycoidodontidae, and probably the Protoceratidae.

This locality is the southernmost point in the Western Hemisphere at which members of the last three of these families have been found (the Equidae reached South America during the Pleistocene). It must be nearly the southernmost point in the Western Hemisphere reached, in Tertiary times, by land mammals moving across a continuous land area, as contrasted with forms, such as rodents, primates, and raccoons, that reached South America by island hopping (*1*). The fossil material now available indicates that the mammals of the Cucaracha Formation were undifferentiated members of a well-established North American fauna; four of the five recognizable genera in the collection are congeneric with forms found widely in North America, and the fifth belongs to a North American family. As regards the larger herbivores, at least, this information lends no support to Simpson's suggestion (*1*) that "Middle America must have been an important center of regional faunal differentiation within the North American general fauna," or to Darlington's contention (*5*, p. 285) that Central America was an island throughout much of the Tertiary. The concept that North and Central America were continuously connected during the Tertiary is reinforced by the presence of a Pliocene mammal fauna of North American type in Honduras, described by Olson and McGrew (*6*).

The most common mammal at the Cucaracha locality is a medium-sized selenodont artiodactyl here tentatively assigned to the Protoceratidae. Its lower premolars are unreduced and show no sign of modification and increasing resemblance to the molars. This is a primitive characteristic in selenodont artiodactyls and indicates a stage of evolution that can roughly be called Oligocene. (These fossils bear a familial resemblance to *Protoceras*, a well-known artiodactyl of the late Oligocene of the High Plains; the premolars of *Protoceras* are more reduced, and thus the genus is probably more advanced, than is the Panama genus.)

The rhinoceros material from the Cucaracha consists of a partial lower jaw of a young individual, a separate lower molar, one and one-half upper molars, a lower premolar, a first upper incisor, and a few fragments of limb bones. The upper incisor, an anteroposteriorly elongated tooth, is typical of the true rhinoceroses (family Rhinocerotidae) as opposed to the extinct families Hyrachyidae, Hyracodontidae, and Amynodontidae. The conformation of the upper incisor and the degree of complication of the upper molars are consonant with a Miocene age. The specimens are assigned to the genus *Diceratherium*, which was widespread in the North American Miocene.

Two upper cheek teeth of horses are present in the collection. Both are brachydont (low-crowned), and therefore come from horses that subsisted by browsing rather than by grazing. Two genera are represented. The larger tooth belongs to *Anchitherium*, known from the Lower and Middle Miocene of North America, the Middle and Upper Miocene of Europe, and the Miocene of Asia. The Florida tooth is in an early stage of wear. A constriction separates the protocone from the protoconule. The hypocone is separated from the metaconule, but would be connected with it after additional tooth wear. The hypostyle is triangular and appressed against the posterior side of the metaloph. In these characteristics the Panama *Anchitherium* represents an evolutionary stage similar to that of *Anchitherium agatense* (Osborn) of the Lower Miocene of Wyoming and Nebraska. It appears to be slightly more primitive than *A. clarencei* Simpson of the late Lower Miocene of Florida and *A. navasotae* (Hay) of the late Lower Miocene of Texas.

The smaller of the two horse teeth is almost unworn. It is assigned to *Archaeohippus*, a small browsing horse found in Miocene deposits of the Pacific coast, Rocky Mountain region, High Plains, Gulf Coast, and Maryland. In the course of evolution of *Archaeohippus* additional folds of the tooth enamel, especially of the hypostyle and crochet, tended to close the enamel lakes (pre- and postfossettes) that would eventually become a major feature of the horse tooth. In the Panama *Archaeohippus* this process had reached about the same stage as that seen in *A. blackbergi* (Hay) of the late Lower to early Middle Miocene of Florida and the late Lower Miocene of the Texas Gulf Coastal Plain.

The family Merycoidodontidae (oreodonts) is represented by the lower jaw of a very large adult and by the badly crushed skull and lower jaw of a young animal.

The adult specimen is 275 millimeters long, exceeding in length all but a few of approximately one hundred known species of the family. It is assigned to the genus *Merycochoerus*, hitherto known from early middle Miocene beds in Colorado, Nebraska, South Dakota, and Wyoming.

The immature skull has well-preserved molar teeth; the third molars had not yet erupted. The incisors and canines are present but are badly broken. A fragment of the maxillo-premaxillary region shows a longitudinal depression in the premaxillary surface, as in the oreodont *Brachycrus* of the middle and late Miocene of California, Montana, Nebraska, New Mexico, and Wyoming. The lower jaw, however, does not appear to be deep posteriorly, as is typical of *Brachycrus*; it has a more gently curved ventral border and a lower ascending ramus, as does *Merycochoerus*, which may be ancestral to *Brachycrus*. This combination of characters is interpreted to mean that the immature Panama skull represents a transition stage between these two genera. It can thus be placed in an evolutionary series of known range in the North American stratigraphic sequence (*7*). Using the evolutionary stages of oreodonts of the High Plains of the United States as a standard for comparison, we find the immature Cucaracha oreodont to represent the same stage as late Marsland or early Sheep Creek faunas (*8*). This places it in the early middle Miocene—that is, early Hemingfordian time in the North American provincial age sequence.

Age of the Cucaracha Formation

Comparison of the Cucaracha mammals with their nearest known relatives in other faunas leads to the conclusion that they are of early Middle Miocene age. The most advanced evolutionary stage, by comparison with North American faunas, is seen in the Panama oreodonts, both of which exhibit characteristics typical of Middle Miocene members of their family. The *Archaeohippus* tooth could be from either late Lower or early Middle Miocene deposits; the tooth of *Anchitherium* resembles most closely its late Lower Miocene relatives to the north. *Diceratherium* is found throughout the Miocene. The only member of the fauna that is seriously out of line with this restricted age span is also the most common—the unnamed protoceratid, which is probably a relict form surviving, at the periphery of the range of its family, from the Oligocene fauna.

Assignment of an age for the Cucaracha fauna must depend upon those members that resemble the geologically youngest forms found in dated sequences elsewhere. The Cucaracha oreodonts fall in this category, and are thus the basis on which we regard the Cucaracha Formation as early Middle Miocene. This fauna was peripheral to the North American mammal fauna; therefore migration must have been to, rather than from, the Cucaracha area. Accordingly, any animals of pre-Middle-Miocene aspect in the Cucaracha fauna are regarded as relicts.

In contrast to the age assignment based upon mammals, Woodring (*4*, p. 39) assigns the Cucaracha Formation to the early Miocene because he considers both the underlying Culebra Formation and the overlying La Boca Formation (*9*) to be of that age. He bases his view that the Culebra is of early Miocene age on the resemblance of its corals and mollusks to those of the Anguilla Formation of Anguilla in the Lesser Antilles and to corals and mollusks of other formations of the same age, including the Tampa Limestone of Florida. The fauna of the La Boca Formation, including Foraminifera, corals, echinoids, and mollusks, differs little in age, according to Woodring, from the Culebra, but represents a somewhat different facies.

The five mammalian genera of the Cucaracha fauna, all browsing ungulates, represent an herbivorous fauna that was spread during Miocene time from coast to coast in what is now the United States. This fauna is well known in the High Plains and Pacific Northwest but is represented in Coastal Plain deposits only in a few widely scattered localities (Fig. 1). The wide range and apparent homogeneity of the fauna are, however, indicated by these occurrences, even though the specimens known from some of the extremes of the population range are so fragmentary that they contribute little

to the morphology or taxonomy of the group they represent.

The Protoceratidae compose a small family (four or five genera) known from the Oligocene and Miocene of the High Plains of the United States and the Miocene of the Texas Coastal Plain and of Florida (Fig. 1, N1, N2). Their low-crowned teeth, light body build, and tendency to develop horns give the impression that they may have occupied an adaptive zone similar to that of the modern Cervidae. They differ from the latter, however, in that their horns are bony out-growths of the skull rather than antlers. The few known specimens of this family exhibit an amazing variety of grotesque horn forms, suggesting that the family may have included a range of types similar in extent to that of the modern antelopes. Their rarity probably results from their having lived in a woodland habitat, where bones are unlikely to be preserved.

The oreodonts (Merycoidodontidae) are remarkably numerous and widespread in North American deposits of Oligocene through Pliocene age. Until oreodonts were discovered at the Cucaracha locality they were unknown outside of North America, yet they constitute an important element of the fauna in the areas where they occur. In Miocene time they were especially numerous in the High Plains, and in the John Day region of eastern Oregon; they are known from California and have recently been found in Big Bend National Park, Texas (*10*) (Fig. 1, N3), but none has been identified with certainty from the Gulf Coastal Plain or from the eastern United States.

The rhinoceros *Diceratherium* is extremely abundant in the Miocene of South Dakota and Nebraska, and in the John Day region; it has been found in the Gulf Coastal Plain and in Florida (*11*); it occurs as far to the northeast as the island of Martha's Vineyard, Massachusetts.

The browsing horses *Anchitherium* and *Archaeohippus* probably ranged over much of what is now the United States in Miocene time; both have been found at localities on the West Coast, in the Rocky Mountain area, and in the High Plains, as well as on the Gulf Coast, in Florida, and, in the case of *Archaeohippus*, in the Calvert Formation of Maryland. *Anchitherium* also lived, in Miocene time, in Mongolia and, in the middle and late Miocene, in Europe. It is believed to have migrated from North America to the Old World.

The presence of *Diceratherium*, *Anchitherium*, and *Archaeohippus* in Florida, Texas, and Panama hints at the presence of a homogeneous Miocene mammal fauna on the North and Central American coasts of the Caribbean Sea. It is probable that this fauna inhabited a subtropical environment.

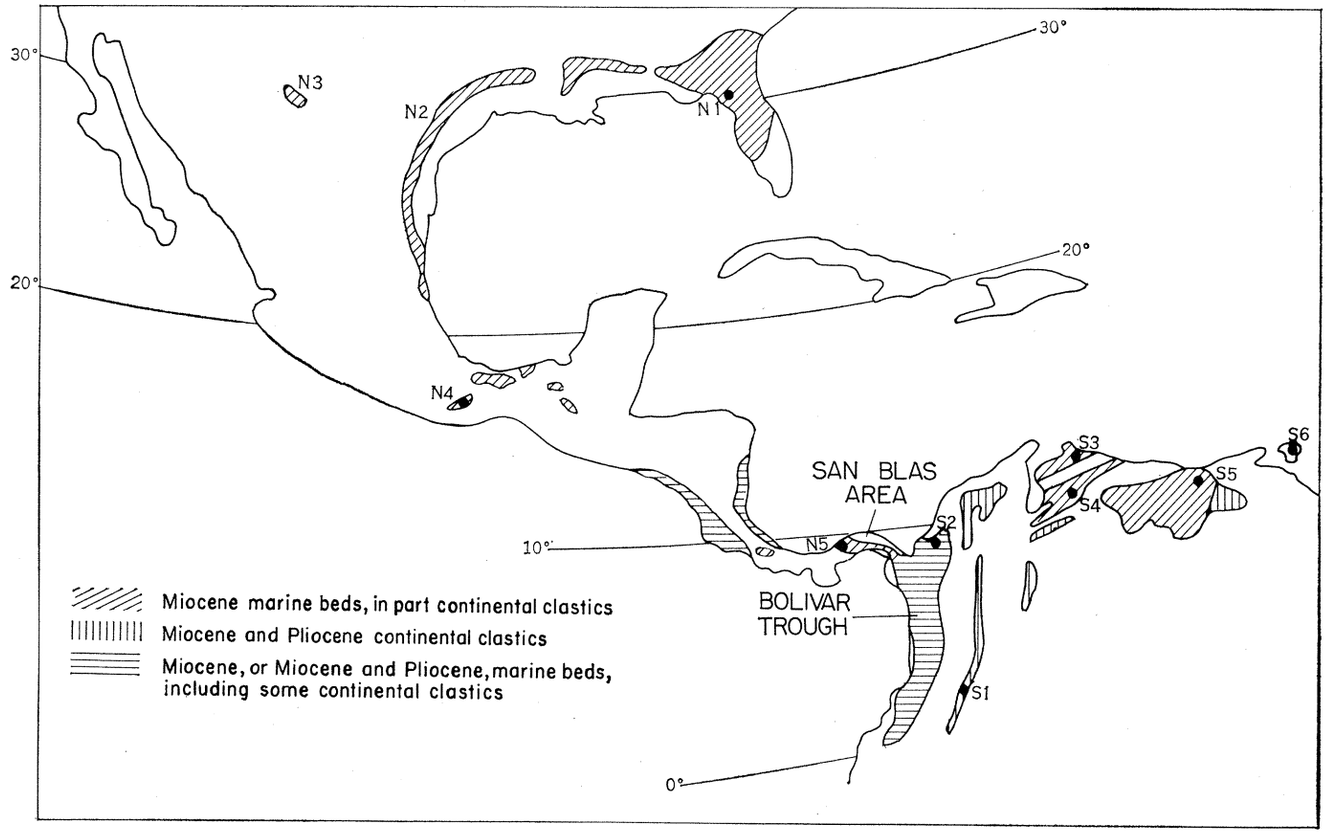

Fig. 1. Miocene land-mammal localities in the circum-Caribbean area. *N*, faunas of North American type; *S*, faunas of South American type. Hatched areas show distribution of Miocene clastic deposits (*19*). (N1) Five North Florida localities, early- to late-Miocene (*20*). (N2) Oakville, Burkeville, Cold Spring, and Lapara faunas, early- to late-Miocene, Texas Gulf Coastal Plain (*11*). (N3) Early Miocene fauna, Big Bend National Park, Texas (*10*). (N4) El Gramal fauna, late Miocene, Oaxaca, Mexico (*21*). (N5) Cucaracha fauna, early middle Miocene, Panama Canal Zone. (S1) Le Venta and Carmen de Apicala faunas, late Miocene, Colombia (*17*). (S2) Peñata fauna, late Miocene or early Pliocene, Colombia (*18*). (S3) Two occurrences, one late Miocene, Pliocene, or possibly Pleistocene, and one probably Miocene, Falcón Province, Venezuela (*22, 23*). (S4) Single Miocene occurrence, western Portuguesa Province, Venezuela (*24*). (S5) Single Miocene occurrence, northeastern Guarico Province, Venezuela (*25*). (S6) Springvale beds, late Miocene, Trinidad (*23*).

Cucaracha Vertebrate Paleoecology

The only associated bones of one individual found in the formation compose the partial, headless skeleton of a large crocodile. Fecal pellets, probably derived from crocodiles, are very numerous. Turtle shell fragments are common. The mammal bones are broken and scattered. A disproportionately large number of them are from young animals. One partial lower jaw of a protoceratid, removed from a concretion, has been deeply etched, possibly by digestive acids; even the tooth enamel has been affected. The Cucaracha sediment contains a considerable amount of detrital quartz. The Cucaracha Formation at the mammal locality probably was deposited in a swamp, the mammal remains deriving from nearby forest (source of the Protoceratidae and horses) and savanna (source of oreodont and rhinoceros). Associated with the vertebrate remains were a few fossil fragments of the wood of *Schwartzia*, a legume that still grows in the area.

Paleogeography of Panama in Cucaracha Time

The presence in Panama of wide-ranging members of the North American ungulate fauna probably indicates that, in middle Miocene time, this portion of the isthmus was connected to North America by a land area of considerable size and stability. This is another argument against the sometimes postulated existence of a Tertiary seaway across the Isthmus of Tehuantepec in southern Mexico (*12*). On the other hand, by contrast with nuclear Central America to the west (Fig. 2), the Canal Zone area was unstable. Marine deposits in the area where the Cucaracha mammal fauna was found indicate inundation by the sea both before and after the time when the mammals arrived there by land from North America. Thus, the area now occupied by the Canal Zone probably was the site of narrow seaways which were closed several times during the Tertiary by uplift of the land.

The age of the Cucaracha mammal fauna seems to indicate that, by early middle Miocene time, extensive emergence had connected nuclear Central America with the area of the present Canal Zone. A possible migration route is shown in Fig. 2. The presence of marine Miocene deposits north of the northwest end of the Talamanca Range (Figs. 1 and 2) may mean that central Costa Rica, as well as the Panama Canal Zone region, was intermittently submerged during the Miocene. The Nicaraguan Depression (Fig. 2) may also have been a transcontinental trough during part of Miocene time. Mammal migration from North America to Panama may have occurred in several stages, as water barriers appeared and disappeared in front of and behind the migrants, but the similarity of the Cucaracha mammals to mammals of North America indicates that such barriers were short-lived.

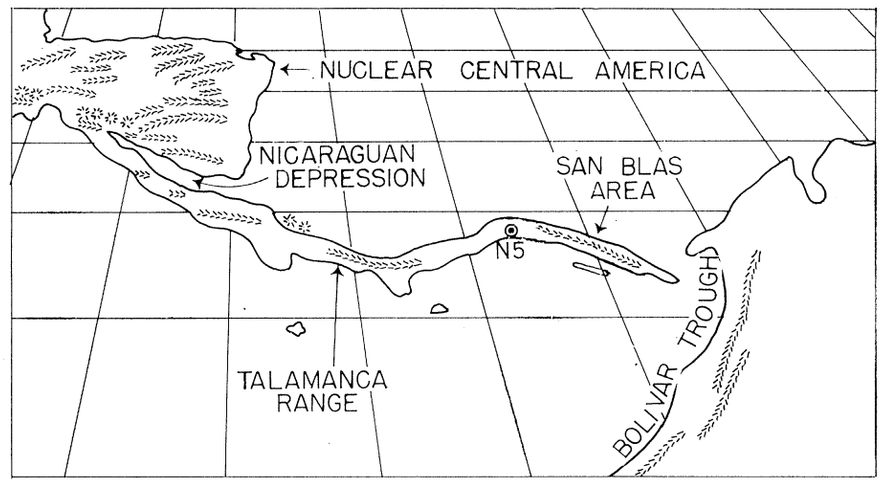

Fig. 2. Southern Central America and northwestern South America in early middle Miocene time. (N5) Cucaracha Miocene mammal site. [Modified from Lloyd (*3*) and Jacobs, Bürgl, and Conley (*26*)]

The presence of North American mammals at the Cucaracha locality also requires reconsideration of the paleogeography of the area east of the site. Lloyd (*3*) and most earlier workers have regarded the arc of eastern Panama from the Colombian border to Gatun Lake as a part of the South American continent that did not participate in the instability which marked the Tertiary history of the isthmian strip. However, the existence of the Bolivar Trough through most of Tertiary time indicates that this area, previously called the Panama Spur, was not connected to the South American continent until the very late Tertiary. It existed, rather, as a large stable island which was at times connected to the land mass to the west, the Talamanca Range (Fig. 2). Since the term *spur* emphasizes the attachment to South America, this stable region is here designated, instead, the San Blas Area (Figs. 1 and 2). The distribution of marine sediments in the region (*4*, p. 10) indicates that the San Blas Area was an island in both early and late Miocene time; in early middle Miocene time, when the Cucaracha mammal fauna lived, it was connected to the stable area to the west (Fig. 2).

In discussing the Bolivar Trough (Fig. 1), Olsson (*13*) points out that Miocene mollusks of distinctly Caribbean character are found as far south as northern Peru, and that faunal intermingling between Atlantic and Pacific took place through the Miocene along this geosynclinal area, which was 100 to 160 kilometers wide. B. F. Uhl (*14*) has not yet found evidence of intermingling of Caribbean and Pacific forms in the foraminiferal faunas of the upper middle Miocene of the Bolivar geosyncline. Partly on the basis of lack of such evidence, Nygren (*15*) concludes that the Bolivar Trough was closed from upper Miocene to Recent time. As a result of his study of the distribution and thickness of marine and terrestrial sediments in the Bolivar geosyncline, Nygren is of the opinion that migration of terrestrial animals could have taken place through the area between upper Cretaceous and middle Eocene time; during the middle Oligocene, the lower Miocene, and the middle Miocene; and between the upper Miocene and the Recent. Such conditions in the Bolivar area may have facilitated migration of the few mammals designated by Simpson (*1*) as ancient immigrants (early Paleocene), old island hoppers (late Eocene and Oligocene), and late island hoppers (middle Miocene through Pliocene);

but faunal evidence, both fossil and Recent, indicates that general movement of fauna between the continents did not take place during these intervals.

During periods of emergence of the Bolivar Trough, its northern and southern extremities appear to have been the last areas to rise above sea level (*16*). Thus, the trough could have been a barrier to intercontinental migration even during the last stages of emergence. When the Bolivar Trough was not a barrier, other barriers, possibly including climatic ones, apparently were operative during most of Tertiary time. The idea of climatic barriers is appealing because *Dicerathertum* and *Brachycrus*, of the Cucaracha fauna, certainly were not tropical forms, occurring as they did as far north as Massachusetts and Montana, respectively. Darlington (*5*, p. 593), on the basis of the present distribution of birds and the past history of mammals, concludes that no important tropical area was attached to North America during the Tertiary. The composition of the Cucaracha fauna supports this conclusion. The northern edge of the neo-tropical realm of Miocene time may have been, as Nygren (*15*) implies, in the northern part of the Bolivar geosyncline.

The contrast between Central American and South American Miocene mammal faunas is particularly sharp when one compares the mammals from the Cucaracha locality (Fig. 1, N5) and those of the La Venta fauna of Colombia (Fig. 1, S1), a varied assemblage of late Miocene mammals, composed completely of South American forms (*17, 18*). The other South American localities plotted in Fig. 1 represent occurrences of only a few mammal bones, most of them of uncertain age, and further emphasize the paucity of Tertiary land mammals in the circum-Caribbean area.

Summary

The presence of Miocene mammals of North American affinity in the Panama Canal Zone indicates that Central America was attached to North America. That this attachment was a broad and stable land mass is shown by the close relation of the Panama Miocene herbivores to the widely distributed Miocene herbivore fauna of North America. A continuous connection existed probably throughout the Tertiary, to the west and north of the isthmian region, but the tectonically active isthmus probably was broken up into an archipelago during most of Tertiary time. Between the islands ran the Strait of Panama; from time to time parts of the isthmian area were connected to the stable land to the west, allowing eastward migration of land animals. The mammals of North American affinity in the Cucaracha Formation were found only a few kilometers from the western end of the San Blas Area, a stable land mass in eastern Panama that was separated from South America by the Bolivar Trough during most of the interval between Oligocene and Pliocene time (*16*). The Strait of Panama was a less stable barrier than the Bolivar Trough; this being so, it is likely that the San Blas Area was inhabited by land animals of North American rather than South American affinity. Thus, the disappearance of the Bolivar seaway in Pliocene time would have allowed, probably for the first time, mingling of the North and South American mammal faunas.

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